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THE HABITS AND MOVEMENTS OF THE RAZOR-SHELL CLAM, ENSIS DIRECTUS, CON.

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Many of the older naturalists have called attention to the sensitiveness and remarkable activity of this form, and the consequent difficulty that is sometimes experienced in capturing it. Some of the observations are not strictly accurate but they have served to call attention to its adaptation for a burrowing life. Even the uncommon shape of the animal indicates this adaptation

The species under consideration is to be found more or less abundantly all along the eastern coast of the United States. It is best known on sandy flats from which most of the water flows at low tide, where specimens may be dug with spade or clam-hoe. In some localities, as in restricted areas around Woods Holl and North Falmouth, Massachusetts, where most of these observations were made, the animals are quite abundant, and in such places one may find the protruding posterior ends of the shells, or see the siphon openings of the undisturbed individuals. They readily take alarm and even a slight jarring of the mud of the bottom in their vicinity serves as a signal for them to instantly disappear. It is this sudden disappearance that has attracted wide attention, and has given the impression that the animals are exceptionally hard to capture (5 and 6).

The species is probably not restricted to very shallow water. Specimens are not often taken in a dredge, but the position that they occupy buried in the rather hard sand or mud of the bottom, makes their capture unlikely. Young specimens, from a millimeter to a centimeter in length have been taken in large numbers

near South Hapswell, Maine, in from ten to thitry feet of water, by means of a fine wire dredge. Supposedly where conditions are right for individuals to grow to a centimeter in length, larger ones would thrive also.

The usual position for undisturbed specimens is with the posterior ends of the shells protruding just above the surface of the mud. Sometimes specimens are found with several centimeters of their shells protruding, but this is not very common. Again all that indicates the presence of a specimen, may be the depression at the spot where the animal has disappeared. The most conspicuous parts of a specimen in its normal position are the siphons, the openings of which appear as nearly round apertures surrounded by tentacles (Fig. 5). Close observation is necessary to see such specimens, as the color of their siphons is almost exactly the same as the bottom where they occur.

Specimens that have their posterior ends protruding above the surface of the mud seem to be more common where the water has drained entirely away than where the flats are still covered with water. Shells are not uncommon on the flats and shores, but they are seldom found embedded in the position that the animals occupy during life. These observations are of especial interest in view of the fact that animals in aquaria quite universally push up out of the mud before they die. The heat of the sun on the bare mud flats is probably disturbing and may cause them to react in the same way they do before they die. If animals react in nature as they do in aquaria, it is natural that the shells of dead animals should be found on the surface.

Specimens are not easily studied in their native places because of ripples on the water and because the character of the bottom makes it hard to approach closely without disturbing them. Walking on the mud near them will cause them to withdraw their siphons or disappear beneath the surface. It has accordingly been more satisfactory to study specimens in aquaria that contain several inches of sand or mud from the bottom from which the specimens were obtained. The animals do not live well in aquaria, even when supplied with running water, but for several hours after they are collected, they remain very active and seem to be quite normal.

If a specimen is touched it will either withdraw its siphons anp

remain quiet until disturbed again, or it will immediately vanish beneath the surface of the mud. If a specimen is grasped and pulled upward there is an immediate response that is so powerful that the animal frequently escapes and disappears. This fact Tryon (6) mentions, saying: "It may often be seen at low tide projecting a little above the level of the sand but, if touched or disturbed, it descends with astonishing rapidity and force, much to the amazement of him who may lay hold of it thinking to make an easy capture." These observations indicate that the animal probably habitually keeps its foot protruded some distance out of the shell to be ready for disturbances.

Specimens taken in firm sandy soil, where the depth can be noted, are frequently found several inches below the surface. Verrill and Smith (7) report that this species digs somewhat permanent burrows that extend nearly perpendicularly into the sand to the depth of three feet, and Woodward (8) states that the animals never voluntarily leave their burrows. I have never been able to demonstrate permanent burrows in the localities where I have worked, but the usual muddy character of the bottom was not satisfactory for the purpose. I doubt, however, if such burrows are habitually constructed. The character of the bottom where they live is frequently not suitable for permanent burrows unless something like a tough secretion is added to the mud to keep it in place, and such a secretion does not seem to be formed. Specimens in aquaria never seem to construct anything like permanent burrows.

As individuals are known to burrow to some depth it is probable that in digging for them, those in the immediate vicinity are disturbed and burrow beneath the reach of the shovel. Verrill and Smith (7) call attention to how easily disturbed they are and say: "When thus alarmed it is generally useless to try to dig them out, for they quickly descend beyond the reach of the spade." Dr. J. Gwynn Jeffreys as quoted by Tryon (6) reports them as having exceptional powers for detecting disturbances. He says: "They are evidently sensible to vibratory movements in the air, as well as on ground, taking alarm at greater or less distances according to the state of the atmosphere and the direction of the wind." It is hard to verify these observations and I am inclined to think they are not accurate, but there can be no

doubt that specimens are easily disturbed by vibrations of the bottom. That they habitually burrow to some depth is indicated by the fact that after the first half dozen trials, specimens are not usually obtained without going to another spot several feet away, although the first trials may have resulted in one or more specimens each.

When dug from the mud, individuals frequently leap or swim. In leaping the shell may be thrown several inches by the action of the foot. In swimming the animal progresses posterior end first and large specimens may swim several feet before stopping. The foot is always active while the animal is swimming. These activities, together with the movements of burrowing, will receive attention later.

Before describing the movements it is desirable to call attention to some points of anatomy.

The shell is of nearly even diameter both dorso-ventrally and laterally (Figs. 1 and 4), throughout its length, except very near its ends. Anteriorly it contracts in both directions a little, but the anterior margins of the shell valves remain wide apart even when they are in contact along their ventral borders (Fig. 6). This leaves ample space for the protrusion or withdrawal of the foot when the shell is closed. The anterior margins of the lobes of the mantle are thickened and extended, so, when the foot is withdrawn into the shell, these flaps cover the opening between the shell valves (Fig. 6). When the foot is extended the flaps are spread apart and form a collar around the foot, the free margins of which are in contact with the foot (Figs. 1 and 4). The collar is thick and muscular, being well supplied with the radial pallial muscles, and as it is held tightly against the foot, forms a very effective scraper, that cleans the foot so mud is not drawn into the shell with it. The cilia covering the foot no doubt aid in loosing the mud so it is easily scraped off. The flexible collar adapts itself to the shape of the foot so its margin is applied to the surface of the foot until its very extremity is drawn into the shell (Figs. 6 and 7).

The posterior end of the shell narrows laterally, but here again the margins of the shell valves are wide apart when the ventral edges of the valves are in contact (Fig. 5). This makes it possible for the siphons to be at least partially extended when the

shell is closed. The reason for this arrangement is found by studying the movements of burrowing and swimming.

The siphons have nearly circular or slightly elliptical openings, and are separated near their extremities. The whole posterior end of the mantle, bearing the siphons, may be protruded some distance beyond the posterior end of the shell. Sense tentacles surround the siphons near their bases and occur on the mantle dorsally and ventrally near the posterior end, where the mantle is exposed between the shell valves (Figs. 2 and 5). Small sense tentacles occur on the surfaces of both siphons, and the branchial siphon bears a number along its extremity that tend to radiate in over the opening of this siphon. The margin of the cloacal siphon has no tentacles. Verrill and Smith have (7) described a definite arrangement for the tentacles but it is doubtful if this arrangement always holds.

The ventral margins of the mantle lobes are united throughout their length except near the middle of the length of the animal, where a small opening remains that is situated just posterior to the retracted foot (Fig. 4). This opening is surrounded by a single row of sense tentacles. Except for this opening, the opening through which the foot is protruded, and the openings of the siphons, the mantle forms a closed chamber.

The united mantle margins are very muscular, being provided with strong circular and radial pallial muscles that are very similar to the muscles of the mantle margins in *Solenomya* (2) where they serve very much the same purpose, that is, to close the shell tightly and to obliterate a portion of the mantle chamber. Like *Solenomya* the valves of the shell are covered with a very heavy, elastic cuticle that is extended beyond the calcareous margins. Mud does not readily adhere to this cuticle. When the valves are closed the cuticle is bent in over the hard margins of the shell (Fig. 8), thus allowing the united margins of the mantle to be withdrawn. Probably this elastic cuticle aids in opening the mantle chamber when the muscles relax, as is undoubtedly the case with *Solenomya* (2), but the effect in this form is certainly much less than in *Solenomya*.

Both adductor muscles are present. The anterior adductor is very large and strong. The posterior adductor is quite small and does not seem to function actively. The united margins of

the mantle posterior to the ventral opening are especially muscular and seem to replace the posterior adductor in function to a marked extent.

The foot, when retracted into the shell, is nearly cylindrical and together with other organs completely fills the part anterior to the ventral opening in the mantle. The dorsal portion of its extremity is pointed, and a slight ridge marks the boundary of what may be called the sole (Fig. 2). The foot is very powerful and remarkably active, its movements being very unlike the slow movements of the foot in most lamellibranchs. It may be thrust from the anterior end of the shell to a distance exceeding one half the length of the shell, and in this position the end may be swelled into a knob or bulb that considerably exceeds the diameter of the shell (Fig. 1). The knob is not cylindrical but is extended dorso-ventrally and laterally and the free extremity or sole is comparatively flattened. In this swollen condition the end of the foot forms a very efficient anchor, as will be found by grasping a shell and trying to withdraw it from the mud. The resistance of the expanded foot is so great that the foot is frequently torn away from the shell when the shell is jerked quickly (7). The foot is attached to the shell by two pairs of foot muscles, both of which are strong and aid in withdrawing the foot into the shell. With the end of the foot anchored, the obvious result of the contraction of these muscles is to pull the shell into the mud up to the position of the bulbous portion of the foot.

For our present purpose it is not necessary to give more attention to the anatomy of the animal, and we will proceed at once to the study of the movements.

Burrowing. — The movements of burrowing may be best studied either in specimens placed in shallow dishes of sea water, which are very likely to execute the movements soon after they are placed in the water, or in specimens held with the anterior end pointing downward and stimulated to activity by stroking the sense tentacles around the ventral opening in the mantle and around the siphons. Specimens in the water are more normal in their movements than the specimens held and stimulated as described. Apparently the action of gravity may cause the held specimen to protrude its foot and to partially expand the end of

it, in which position the foot may remain quiet for some time. When the movements are active they are essentially the same in both cases. The foot is slowly protruded with the pointed tip working as if trying to bore into the mud, ending each time with a dorsal thrust. These movements are continued until the foot is fully extended. During this extension the end of the foot is kept small, the point is directed well forward, and the general diameter of the protruded part of the foot is decidedly less than its normal diameter when at rest. When the foot reaches its greatest extension, the end is suddenly swelled into a great bulb, more than twice the diameter of the remainder of the foot (Figs. 1 and 4) and the whole foot becomes very rigid. That this result is attained by injecting blood into the foot may be readily proved by sticking spring forceps into the end of the foot so the spring will hold the wound open, and stimulating the foot to activity by stroking the tentacles as before described. When the foot starts to become active the wound begins to bleed rapidly, and when the final effort to swell the end of the foot is made, the blood rushes out in a great jet, but the swelling is slight. A simple incision does not answer as well, as the contracting muscles seem to close the wound more or less perfectly.

The instant that the swelling of the end of the foot is complete, a process that takes place so rapidly as to be almost startling, the retractor muscles pull the foot back to the shell with a jerk, the end remaining swollen until it reaches the shell (Fig. 7). It is then reduced in size and either withdrawn into the shell or extended in the beginning of a new burrowing movement.

While the foot is being extended the shell valves are allowed to gap apart and the siphons and ventral opening in the mantle are kept more or less widely open. Just before the final sudden retraction, the siphons and ventral opening are all tightly closed, and kept so until retraction is complete. The result is that the water in the mantle chamber is discharged through the opening through which the foot is extended, between the collar and the foot. Whether the water escapes all around the foot or only ventral to it, where the contact of the collar is poorest, has not been determined, but the jet of water is quite powerful. When the shell is embedded in the mud, each retraction of the foot,

squirts the water against the mud ahead of the shell, the shell is decreased in diameter by being closed, and the mud is dislodged and washed up the sides of the shell where it may be seen raising after each downward movement of the shell. The action is similar to the pile driver that opens a way for the pile by a somewhat similar stream of water.

The burrowing movements may follow each other quite rapidly but the extension of the foot is never very rapid, as it must be carefully worked into the mud to keep from forcing the shell back. The opening of the shell just before the extension of the foot, tends to embed it more firmly and thus to hold it in position while the foot is being worked into the mud.

A specimen laid on its side on mud, has no difficulty in gaining a hold with its foot that enables it to right itself and start the anterior end into the mud. Burrowing is then normal, and the shell is soon completely buried. The time necessary for a specimen to completely bury itself varies with the character of the mud. In soft mud the thrusts may be rapid and few are needed, in hard sand the thrusts will necessarily be slower and more movements are required, but even in such material the animal will disappear very promptly. When the animal is laid on its side on such sandy mud as that in which it usually lives, one movement will frequently suffice for it to right itself, and four or five more will carry it out of sight. The time necessary for this may be less than half a minute. Embedded as the animal usually lives, a single retraction takes it out of sight and away from enemies.

Swimming. — It is more difficult to study the movements of swimming, as animals swim only occasionally, and then generally immediately after being dug, and the movements of parts of the animal, and the animal as a whole, are so rapid as to make accurate observations difficult. The following points have been determined however and, from these, conclusions may be drawn: (1) The animal progresses posterior end foremost; (2) movements are by jerks, each jerk carrying the animal one or more times its length; (3) the foot is very active, being thrust out and withdrawn repeatedly. The outward thrust is comparatively slow but the withdrawal is extremely rapid; (4) apparently the valves of the shell are drawn together every time the foot is re-

tracted; (5) each movement of the animal as a whole, corresponds to the period of retraction of the foot.

In describing the movements of burrowing it has already been mentioned that water is thrown from the shell, through the opening through which the foot is protruded, every time the foot is retracted into the shell. Each jet is caused by closing the other openings into the mantle chamber and driving the water out by pulling the foot in, by closing the shell by the contraction of the adductor muscles and the united margins of the lobes of the mantle, and by drawing the mantle margins, with the shell cuticle to which they are attached, into the mantle chamber (Fig. 8). The resultant action is to drive out most of the water that was between the valves of the shell, as nearly all of the space is now occupied by organs of the body. As all of the openings except the one around the foot are held closed, a very strong jet of water must be forced out around the sides of the foot. This is sufficient to cause the movement of the animal in the opposite direction. Many muscles, all of which are powerful, are used in this action, and as the water is thrown through a small opening between the muscular collar and the foot, the resulting force is considerable. The action, so far as movement is concerned, is similiar to what is so well known in the squid, and differs from the movement of *Solenomya* only in direction (2). Here the movement is posterior, in *Solenomya* the movement is anterior. Here the water is admitted through the siphons, and possibly also around the foot, and then, with the siphons closed, the water is thrown from the anterior end of the animal. In *Solenomya* the water is admitted around the foot, which opening is then closed and the water is thrown through the posterior opening. The method of forming the jet is quite the same in both animals. In both forms the same organs are used, but in *Solenomya* more use is made of the mantle margins and less of the retraction of the foot than is the case in this form.

Throwing strong jets of water from the siphons must aid lamellibranchs in keeping their mantle chambers clean. Some forms need to throw more powerful jets than others because the conditions under which they live demand it. A diversion of this use is apparently to be seen in the forms that swim either by

clapping the shell valves together, as in the case of *Pecten* (3), or by the more complicated method used by *Solenomya* and the form under consideration. It is likely that the jets thrown by this form are of very secondary importance, so far as swimming is concerned, and that their chief function is to aid the animal in burrowing. This is indicated by the fact that the jets are thrown from the anterior end of the shell, while in forms that use them for cleaning the mantle chamber only, they are thrown from the siphons.

Leaping. — Leaping may consist simply of a sudden, powerful protrusion of the foot, in which case the animal generally turns so as to lie somewhat nearly on its dorsal margin and catches the tip of its foot in the mud as it is protruded. The shell is thus thrown posteriorly. Generally, however, the foot is bent back under the shell, which is turned partly over towards its dorsal margin (Fig. 3) and is then suddenly made rigid with the result that it straightens out with great rapidity. This may result in projecting the animal backward, or in certain cases the foot may catch so as to turn the shell more or less completely end for end. Leaping movements are usually rapidly repeated several times when they are once begun. In many ways they resemble similar movements in *Yoldia* and *Solenomya* (2), but the foot of this form is so much longer that the impression of much greater activity is left with the observer.

The perfection of the movements of burrowing by a form that lives in the mud, so it may be able to escape its enemies, is of so much importance as to need no comment. When combined with sense organs that give immediate information of the presence of enemies, and with protective coloration that hides it from its enemies until they shall have given it warning, the rapid burrowing movements form a striking adaptation.

The uses of the swimming and leaping movements are not quite so evident. Small razor-shell clams have been taken in tow nets at the surface of the sea. The ability to swim is, then, sufficient to make it possible for the young specimens, at least, to change their positions after settling to the bottom, and after the larval locomotor organ, the velum, has been lost. If the first location does not offer the necessary food or bottom conditions, it is pos-

sible to move. Although the machinery for this is rather clumsy, and was primarily designed for another purpose, that of burrowing, it might be the deciding factor in the struggle of life. The fact that young specimens may be taken at the surface of the water, even the fact that the animals are able to swim at all, indicates that they probably occasionally change their positions. The statement made by Woodward (8) that the animals never voluntarily leave their burrows seems doubtful. They certainly do leave the mud when they are about to die, and there is no reason to believe that they might not voluntarily move from one place to another should occasion require.

Leaping may aid the animals in getting free from certain kinds of bottom or even occasionally in escaping enemies, should they be removed from the mud in any manner. Not infrequently specimens that have been swimming might become lodged so they could not burrow without changing their positions, and then the leaping movements would be of advantage.

Summary.

The animal is very active, burrows with great rapidity, and may also swim and leap.

In burrowing, the foot is worked into the mud as it is protruded, the end is then swelled into a knob, and by its sudden withdrawal the shell is drawn to the position of the anchored end of the foot. Simultaneous with the retraction of the foot, a strong jet of water is thrown from the anterior end of the shell, so the mud is softened or even washed away as the shell descends, an action similar to that of some of the modern pile drivers. A collar, formed by the anterior end of the mantle, surrounds the foot and acts as a scraper that prevents mud from being drawn into the shell with the foot.

The animal is able to swim by throwing jets of water from the anterior end of the shell, thus progressing backward by a series of jerks.

By the uncommon activity of the foot the animal is able to throw itself about on the bottom.

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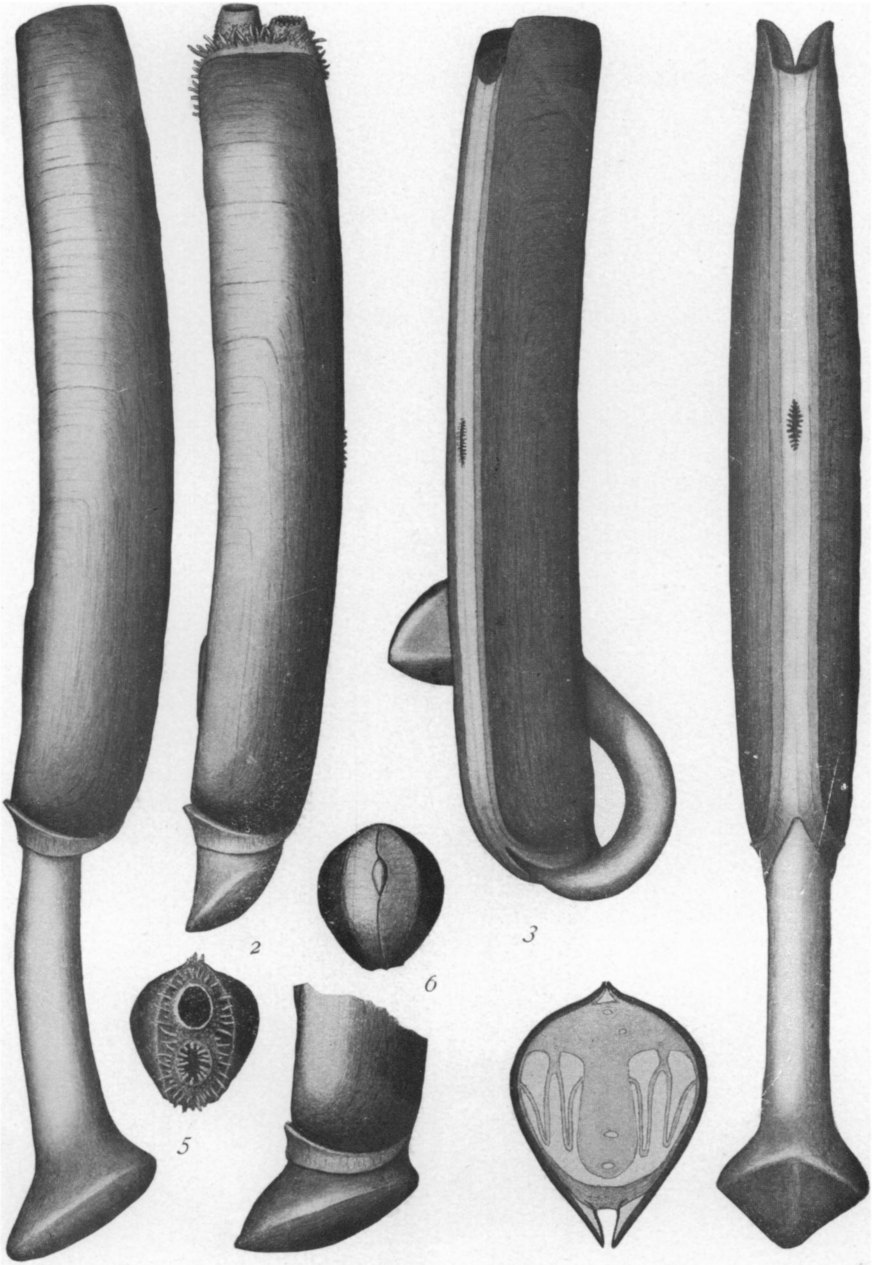
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Explanation of Plate II.

Fig. 1. A specimen with the foot extended and the end of the foot swelled, the instant previous to withdrawal. Drawn with the aid of an instantaneous photograph made by Mr. J. G. Hubbard of a specimen held with the anterior end down, and stimulated into activity. Natural size.

Fig. 2. A specimen showing the usual position assumed in a dish of sea-water. The siphons may be extended more than is shown in this figure. Drawn from observations. Natural size.

Fig. 3. A specimen showing the position assumed just before leaping. Drawn from observations. Natural size.

Fig. 4. Ventral view of a specimen that has the foot extended to the position shown in Fig. 1. Drawn from observations. Natural size.

Fig. 5. Direct view of the posterior end of an animal that has the siphons extended. Drawn from observations. Natural size.

Fig. 6. Direct view of the anterior end of a specimen that had withdrawn all but the tip of the foot, showing the adjustment of the collar. Drawn from observations. Natural size.

Fig. 7. Anterior end of a specimen showing the position and shape of the foot at the end of a burrowing movement. Drawn from observations. Natural size.

Fig. 8. Diagrammatic cross section of an animal, taken just posterior to the ventral opening in the mantle, to show how the mantle chamber is diminished by the contraction of the united mantle margins. Twice natural size.